COURTSHIP AND MATING BEHAVIOR OF BRACHYPELMA KLAASI (ARANEAE, THERAPHOSIDAE)

Martha Yáñez and Arturo Locht: Laboratorio de Acarología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Coyoacán 04510, D.F. México

Rogelio Macías-Ordóñez: Departamento de Ecología y Comportamiento Animal, Instituto de Ecología, A.C., Xalapa, Veracruz 91000, México

ABSTRACT. Courtship and mating behavior of *Brachypelma klaasi*, heretofore unknown, is described on the basis of three courtship and mating sequences, one in captivity and two in the field. Adult males perform courtship movements (pedipalp drumming, leg drumming, push-up and shaking) when they locate a female's burrow, probably in order to avoid female aggression. After some physical contact, the female raises the prosoma and extends her chelicerae. The male then grasps her chelicerae with his tibial apophyses and the female arches her body backwards leaving the epigynum exposed. The male starts boxing the female's sternum and presumably inserts his pedipalps and inseminates the female. In two cases the female vigorously attacked the male immediately after mating and probably would have killed him had observers not intervened; the other pair separated more slowly and peacefully. Males appear to use chemical and/or tactile cues from the female's silk around the burrow during short-range searching behavior. Males begin courtship behavior by drumming on the silk to signal to the female that he is present. One male of *B. klaasi* observed in the field laid silk over the female's silk around the burrow, possibly to prevent subsequent matings by other males. A second male did not detect the burrow after this act.

RESUMEN. Se describe el cortejo y apareamiento de *Brachypelma klaasi*, hasta ahora desconocidos con base en tres secuencias de cortejo y apareamiento, una en cautiverio y dos en campo. Los machos adultos realizan movimientos de cortejo (tamborileo con pedipalpos, tamborileo con patas, lagartijas y temblado) cuando localizan nidos de hembras, probablemente para evitar la agresion de las mismas. Después de un periodo de contacto físico la hembra levanta el prosoma y evierte los quelíceros. El macho prende los quelíceros de la hembra con sus apófisis tibiales y la hembra se arquea hacia atrás exponiendo el epigineo. El macho boxea contra el esternón de la hembra y se asume que inserta sus pedipalpos y la insemina. En dos casos la hembra atacó al macho inmediatamente después del apareamiento y probablemente lo hubiera matado de no haber intervenido el observador, la tercera pareja se separó más lenta y pacíficamente. Aparentemente los machos utilizan señales químicas o tactiles de la seda de la hembra alrededor del nido durante la búsqueda de corto alcance. Los machos inician el cortejo tamborileando en la seda, probablemente para anunciar su presencia a la hembra. Un macho de *B. klaasi* observado en el campo depósito seda sobre la de la hembra alrededor del nido, posiblemente para evitar copulas subsecuentes de otros machos. Un segundo macho no pareció detectar el nido después de la conducta mencionada.

Tarantulas (Mygalomorphae, Theraphosidae) are highly diverse in Mexico, with many species distributed in restricted, endemic areas (Yáñez & Locht 1997). The genus *Brachypelma* contains nine species distributed along the Pacific coast of Mexico, eight of which have small, discrete ranges. At least one of these species, *Brachypelma klaasi* (Schmidt & Krause), and possibly more, are being considered for inclusion as endangered species under CITES.

Consequently, studies of reproductive behavior are important to aid in their reintroduction to their natural environment. Furthermore, few studies have been conducted on the reproductive behavior of tarantulas in general, and little of the literature that has been published contains detailed behavioral descriptions (though see Stradling 1994; Shillington & Verrell 1997). Studies that describe reproductive behavior either partially or in detail have been undertaken on the following genera: *Dugesiella* (Baerg 1958; *Petrunkevitch* 1911), *Eurypelma* (Baerg 1928), *Cyrtopholis* (Petrunkevitch 1934), *Aphonopelma* (Bücherl 1971; Herrero & Valerio 1986; Minch 1979;

Shillington & Verrell 1997), *Grammostola* (Pérez-Miles 1988), *Ceropelma* (Pérez-Miles 1992). Here we provide a detailed description of courting and mating behavior in *Brachypelma klaasi* in the field and in captivity.

Species studied.—The female lays a single egg sac containing 400–800 eggs in her burrow in April-May. The female guards the egg sac for 2–3 months before the spiderlings emerge and disperse. In the juvenile stage, spiders produce temporary burrows until a suitable site is found for a permanent burrow which the spider inhabits for many years. Adult females reach reproductive maturity between 7–9 years and live for up to 30 years. Adult female body size ranges from 50–75 mm and female weight ranges from 19.7–50 g. Males mature earlier (between 6–8 years) and live between 4–6 months. Male weight ranges from 10–45 g (Yáñez pers. obs.).

The female's burrow varies in length from 0.15–2 m, depending on the site and the age of the spider. The burrow complex consists of a horizontal tunnel leading from the burrow entrance to a primary chamber where molting usually takes place, and an inclined tunnel that connects the primary chamber to a larger, secondary chamber where the spider rests during the night and where prey is consumed. The female puts a few silk strands at the entrance of the burrow probably so that a male can detect that a female is present. Once the male has detected the silk strands, courtship behavior may be initiated.

Brachypelma klaasi was originally placed in a new genus, Brachypelmides, by Schmidt & Krause (1994). However, a recent comparative study of morphology and distribution of species within Brachypelma provides much evidence for including klaasi in the Brachypelma group and suggests that Brachypelmides be used as a synonym of Brachypelma (Locht et al. 1999). In order to avoid confusion, we use the name Brachypelma klaasi (Schmidt & Krause).

METHODS

Field studies were conducted at La Estación de Biologia "Chamela", Jalisco, Mexico, situated on the Pacific coast in a tropical deciduous forest (19°30′N, 105°03′W, 200 m). Courtship and mating behavior were observed in two pairs in the field on 23 November 1997. The first description of courtship and

mating (pair 1) was made at 1030 h (temperature 27 °C and 89% relative humidity) when a male (weight = 10 g) was found 4 m away from a female burrow (female weight = 40 g) and placed 10 cm in front of it in order to encourage reproductive behavior. The second description (pair 2) was made at 1700 h (temperature 27 °C and 87% relative humidity) using a male (weight = 30 g) caught several kilometers away from the second female burrow (female weight = 45 g).

A third pair (pair 3) was observed in captivity on 11 February 1998 in an environmental chamber at the Facultad de Ciencias of the National Autonomous University of Mexico in Mexico City (27 °C, 60% RH, 12:12 light cycle) using a male (weight = 27 g) caught on 24 November 1998 and a female (weight = 35 g) caught on 2 October 1997 at the field location. Prior to pairing, the male was kept isolated in a 37.5 1 aquarium with soil from the collection site and small pieces of logs. The female was kept in similar conditions in a 50 1 aquarium. The male was placed in the female's tank to provoke reproductive behavior.

Encounters were videotaped using a Sony Handycam[®] Video 8 recorder. Video records were observed at varying speeds in order to accurately describe behavioral patterns.

RESULTS

Five behavioral patterns were observed in the male. Pedipalp drumming (PD): pedipalps are alternately raised and lowered, about 5 mm off the ground, each cycle lasts between 0.5-0.8 sec. Pedipalp boxing (PB): the male alternately strikes the female sternum with his pedipalps, each cycle lasts between 0.5-0.8 sec. Boxing cycles could not be quantified given the angle of view, since the bodies obstructed vision of ventral interactions between males and females. Leg drumming (LD): the two legs of the same pair are rapidly (0.1 sec) raised and lowered, between 5-20 mm off the substrate; only pairs I (LDI) or II (LDII) are involved in this pattern. Shaking (S): quick (< 1 sec) vibratory movements of the entire body. Push-ups (PU): an instantaneous raise and lowering of the body. No behavioral patterns were observed in the female, except for shaking, which was similar to that of the male.

Although the three reproductive events varied greatly, four stages could be defined: *Male*

approach (MA) begins when the male is placed by the observer near the female's burrow and ends when the female is observed in the entrance of the burrow. Female response (FR) ends when physical contact is established between male and female. Physical contact (PC) ends when the pair separates. Post-mating behavior (PM) comprises any behavior pattern performed immediately after separation.

Pair 1.—Courtship began with the male leg-drumming on the silk surrounding the burrow and shaking his body. The female came out of the burrow 64 sec after the male started drumming. As she approached, the male continued leg-drumming and drummed his pedipalps once. Female response lasted 58 sec from exiting the burrow to engaging in frontal physical contact. During physical contact, the male drummed the substrate and boxed the female, after which she arched backwards and presumably was inseminated (insemination could not be confirmed in any pair given the angle of view since the bodies obstructed vision of ventral interactions between males and females). The female then started pushing down the male, and he retreated gradually, facing her. Within a second of breaking physical contact (which lasted 84 sec) the female attacked the male vigorously, at which point the observer intervened. A drop of sperm was recovered from the female, and microscopic analysis showed a dense mass of what could be reserve substances mixed with sperm cells.

Pair 2.—The male slowly approached the burrow, frequently shaking, and entered the burrow after 261 sec, at which point the female could not be observed. They remained out of sight inside the burrow for 153 sec, after which they came out, engaged in frontal physical contact and remained like this for another 196 sec. During this period the female seemed to be highly receptive, arching the body backwards while the male boxed her, and presumably inseminated her. After a slow separation, the male started to groom his chelicerae while the female returned to the burrow. Then, 128 sec after separation, the male started to spin a thread immediately next to the female burrow for another 60 sec. A second male placed on the silk surrounding the burrow did not seem to locate the female's burrow.

Pair 3.—Immediately after being placed in-

side the female's aquarium, the male started drumming and pushing-up on silk threads spun by the female. He then approached the female from behind, at which point she turned and engaged in frontal physical contact. During physical contact, which lasted for 67 sec, the male boxed the sternum of the female though the number of bouts could not be quantified. The female pushed vigorously down on the male, an apparently aggressive act that made insemination difficult. The female then suddenly attacked the male, at which point the observer intervened. A drop of sperm was observed after separation in the left embolous palp of the male. However, insemination probably did not occur.

Of the three pairs observed, Pairs 1 and 3 displayed similar behavioral patterns compared to Pair 2 (Table 1). The female in Pair 2 was more receptive than the other females observed: the male went into her burrow and brought the female out, she arched completely during mating, and afterwards made no aggressive attempt before returning to her burrow. The other two pairs had shorter physical contact before disengaging, females arched less and pushed the male forward. In both cases the female attacked the male. The two females observed in the field, females 1 and 2. have remained within their burrows, closed with leaves and silk, to the date of submission of this paper (late April 1998) in a fashion similar to that described for other species when they are developing an egg sac (Baerg 1928).

DISCUSSION

Observations of short-range male-searching behavior suggest that males might use chemical or tactile cues from silk spun around the female's burrow. Once in contact with the female's silk, males begin courtship behavior by drumming on the silk to signal to the female that he is present. This behavior has been observed in other theraphosids (e.g., Minch 1979; Costa & Pérez-Miles 1992; Shillington & Verrell 1997). An interesting observation for one male of B. klaasi observed in the field was the laying down of silk over the female's silk around the burrow. It appears that this may be a method of interfering with chemical or tactile cues that may be used by subsequent males to locate the female.

Although minor differences in courtship be-

Table 1.—Duration and behavioral patterns in each stage of the three reproductive interactions observed. Abbreviations are described in the Results section, numbers are frequencies of male behavior patterns, except for FS: female *shaking*. *Pedipalp drumming PD*: pedipalps are alternately raised, about 5 mm off the ground, each cycle lasts between 0.5–0.8 seconds. *Pedipalp boxing PB*: the male alternately strikes the female sternum with his pedipalps, each cycle lasts between 0.50–0.8 seconds. *Leg drumming LD*: the two legs of the same pair are rapidly (0.1 second) raised and lowered, between 5–20 mm off the substrate; only pairs I (LDI) or II (LDII) are involved in this pattern. *Shaking (S)*: quick (<1 second) vibratory movements of the entire body.

| | Male approach | Female response | Physical contact | Post-mating |
|--------------------|---------------------------------------|---|--------------------------------------|-------------------------|
| Pair 1 (field) | 64 sec LDI:2, S:1 | 58 sec PD:1, LDI:5 | 84 sec PD:1, PB:3, LDII:3, S:1 | None (female attack) |
| Pair 2 (field) | 201 sec LDI:20, S:10 | Inside female burrow (not ob- served) | 196 sec PD:1, PB:2, S:6 | 252 sec LDI:2, S:3 |
| Pair 3 (captivity) | 153 sec PD:32, LDI:1, S:4, PU:4 | 116 sec S:20, PD:11, LDI: 9 | 67 sec PB | None (female attack) |

havior were observed among the three pairs of B. klaasi, general aspects of the behavior were similar to those known for other theraphosid species. In particular, the "aggressive" posture adopted by the female by raising her prosoma, followed by the grasping of her chelicerae with his tibial apophyses is characteristic of many theraphosids (Baerg 1958; Minch 1979; Raven 1988; Costa & Pérez-Miles 1992; Shillington & Verrell 1997). It is worth noting that courtship behavior and mating occur outside the female's burrow in B. klaasi as in other tarantula species (e.g., Costa & Pérez-Miles 1992), where there is sufficient space for the female to adopt the raised posture.

Male courting may serve various functions (Coyle 1971, 1985; Jackson & Pollard 1990; Costa & Pérez-Miles 1992; Shillington & Verrell 1997). Courting behavior by the male may inhibit female attack (Barth 1993). Agressive female behavior towards males before, during and after mating is well known in many spider groups (Elgar 1992), as males represent a potential food resource as well as a mating opportunity for females. In the Theraphosidae, cannibalism after mating has been documented for several species (e.g., Bücherl 1951; Shillington & Verrell 1997). However, many studies have observed no sexual cannibalism (e.g., Costa & Pérez-Miles 1992; Stradling 1994), and even in species where cannibalism has been recorded, such events are often rare (Shillington & Verrell 1997). Jackson & Pollard (1990) suggested that sexual cannibalism is generally rare in theraphosids, and that male grasping behavior may be due to factors other than avoidance of female attack. Other potential factors include communication related to mate choice (Coyle 1971, 1985), or simply as a way of maneuvering the female for successful sperm transfer (Coyle 1971; Jackson & Pollard 1990). However, low rates of sexual cannibalism in theraphosids may be a result of male grasping behavior. Without this behavior, cannibalism rates might be significantly higher. While cannibalism is rarely observed in theraphosids, aggresssive female behavior directed towards the male was observed in two of the three pairs of B. klaasi; though whether the attacks would have resulted in cannibalism is unknown as, in both cases, the authors intervened before the male could be injured. Brachypelma klaasi is endemic and has small, isolated populations with limited distributions in parts of the Pacific coast (Yáñez & Locht 1998). The interactions described in this paper were staged given the rarity of the species and the difficulty of observing courtship and mating behavior under natural conditions. Compounding the rarity of B. klaasi, the high value placed on tarantulas in the pet trade has led to high rates of collection and trafficking of species from Mexico, although the extent of trafficking in *B. klaasi* is unknown. Consequently CITES is considering giving *B. klaasi* (and other species in the *Brachypelma* group) endangered status.

Captive breeding and reintroduction of *B. klaasi* is an important means of sustaining natural populations. The studies presented here suggest that mating *B. klaasi* in captivity is not difficult and the production of eggs in the laboratory should be successful under a captive-breeding program. Furthermore, if *B. klaasi*, one of the rarest Mexican tarantulas, can be mated successfully in captivity, and studies of other species have produced similar results (e.g., Shillington & Verrell 1997) reintroductions of captive-bred individuals may be a successful technique for increasing population levels of other tarantula species.

ACKNOWLEDGMENTS

We are grateful to Anita Hoffmann, Juan Morales-Malacara and Graham Floater and two anonymous reviewers for useful suggestions in early versions of this manuscript. James Berry made useful style corrections. La Estación de Biología "Chamela", Instituto de Biología, Universidad Nacional Autónoma de México, provided support during the field work. The Controlled Environment Chambers laboratory in The Facultad de Ciencias, Universidad Nacional Autónoma de México, provided captivity facilities. Financial assistance was provided by Dirección General de Asuntos del Personal Académico, UNAM, Grant No. IN217397.

LITERATURE CITED

- Baerg, W.J. 1928. The life cycle and mating habits of the male tarantula. Quart. Rev. Biol., 3:109–116.
- Baerg, W.J. 1958. The Tarantula. Univ. of Kansas Press, Lawrence, Kansas.
- Barth, F.G. 1993. Sensory guidance in spider precopulatory behaviour- a mini review. Comp. Biochem. Physiol. 104a:717-733.
- Bücherl, W. 1951. Estudios sobre a biología e a sistematica do genero *Grammostola* Simon, 1892. Monog. Inst. Butantan, 1:1-126.
- Bücherl, W. 1971. Los Arácnidos. Pp. 341–344. In Zoología Hispanoaméricana de los Invertebrados (L. Cendrero, ed). Brazil.
- Costa, F. & F. Pérez-Miles. 1992. Notes on mating and reproductive success of *Ceropelma longisternalis* (Araneae, Theraphosidae) in captivity. J. Arachnol., 20:129–133.
- Coyle, F.A. 1971. Systematics and natural history

- of the mygalomorph spider genus *Antrodiaetus* and related genera (Araneae: Antrodiaetidae). Bull. Mus. Comp. Zool., 141:269–402.
- Coyle, F.A. 1985. Observations on the mating behaviour of the tiny mygalomorph spider, *Microhextura montivaga* Crosby & Bishop (Araneae: Dipluridae) Bull. British Arachnol. Soc., 6:320–330.
- Elgar, M.A. 1992. Sexual cannibalism in spiders and other invertebrates. Pp. 128–153. *In* Cannibalism: Ecology and Evolution Among Diverse Taxa (M.A. Elgar & B.J. Crespi, eds). Oxford Univ. Press, Oxford.
- Herrero, M. & C. Valerio. 1986. Análisis de la actividad diaria de *Aphonopelma seemanni* (Araneae, Theraphosidae) en Costa Rica. J. Arachnol., 14:79–82.
- Jackson, R.R. & S.D. Pollard. 1990. Intraspecific interactions and the function of courtship in mygalomorph spiders: a study of *Porrhothele antipodiana* (Araneae: Hexathelidae) and a literature review. New Zealand J. Zool., 17:499–526.
- Locht, A., Yáñez, M. & Vázquez, I. (in press). Notes on the distribution and natural history of the genera *Brachypelma* and *Brachypelmides* (Theraphosidae, Theraphosinae) with comments on morphology and generic affinities. J. Arachnol.
- Minch, E.W. 1979. Reproductive behavior of the tarantula *Aphonopelma chalcodes* Chamberlin (Araneae: Theraphosidae). Bull. British Arachnol. Soc., 4(9):416–420.
- Pérez-Miles, F. 1988. Variación relativa de caracteres somáticos y genitales en *Grammostola mollicoma* (Araneae, Theraphosidae). J. Arachnol., 17:263–274.
- Pérez-Miles, F. & F. Costa. 1992. Interacciones intra e intersexuales en *Grammostola mollicoma* (Araneae: Theraphosidae) en condiciones experimentales. Bol. Soc. Zool. Uruguay., 7:71–72.
- Petrunkevitch, A. 1911. Sense of sight, courtship, and mating in *Dugesiella hentzi* (Girard), a theraphosid spider from Texas. Zool. Jb. (Syst.), 31: 355–376.
- Petrunkevitch, A. 1934. New observations on molting and mating in tarantulas. New York Entomol. Soc., 42:289–296.
- Raven, R. 1988. Preliminary observations on the mating behaviour of the Australian mygalomorph spider *Australothele jamiesoni* (Dipluridae, Araneae, Arachnida). Mem. Queensland Mus., 25:471–474.
- Shillington, C. & P. Verrell. 1997. Sexual strategies of a North American "tarantula" (Araneae: Theraphosidae). Ethology, 103:588–598.
- Stradling, D.J. 1994. Distribution and behavioral ecology of an arboreal "tarantula" spider in Trinidad. Biotropica, 26(1):84–97.
- Yáñez, M. & A. Locht. 1997. El Infraorden My-

galomorphae en México: Una recopilación a nivel mundial. Tesis Conjunta. Facultad de Ciencias, UNAM.

Yáñez, M. & A. Locht. 1998. Ensayos de apareamiento inducido en *Brachypelma klaasi* (Schmidth & Krause, 1994) (Araneae: Theraphosidae). So-

ciedad Mexicana de Entomología. Memorias del XXXIII Congreso Nacional de Entomología. Pp. 37–41.

Manuscript received 1 May 1998, revised 8 January 1999.